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SPECIFIC AND VARIETAL CHARACTERS IN ANNUAL SUNFLOWERS

PROFESSOR T. D. A. COCKERELL

UNIVERSITY OF COLORADO

THE group of *Helianthus annuus*, the typical, annual sunflowers of North America, is not a large one. The annual habit seems to have been acquired independently by several different Helianthine stocks, so that *H. bolanderi* Gray, *H. exilis* Gray, *H. floridanus* Gray and *H. tephrodes* Gray are to be excluded from the *H. annuus* group. The subgenus *Helianthus* s. str., or *Euhelianthus*, contains the following:

1. *H. annuus* Linn. Based on the large cultivated form (*H. macrocarpus* D. C.), Dr. A. H. Church of Oxford has investigated the history of this plant, and I take the liberty of quoting from a letter he wrote on March 4, 1915:

The published accounts of the giant sunflower in Europe in the sixteenth century are so precise that it is interesting to remark that this is in fact the *oldest* mutation known, which is *still* with us, quite unaffected, though still never quite a pure strain, owing to insect pollination. The facts are quite simple. The first description of the plant, by Dodonæus (1567), tells us it grew in the Botanic Garden at Madrid, *24 feet*. At the Padua Garden, *indoors*, in a viridarium or orangery, *40 feet*! The usual height was 20 ft. The first English specimens, grown in London by Gerard, were 14 ft.; and 15 ft. is the local record here. The giant form is known by carrying one *head*, and having no trace of axillary buds, = *Monocephalic* strain, as opposed to reverting branching individuals. . . . The next point is, where did it come from? *From Peru*, say the Herbals, but all Spanish things from America came *via* Peru, because this was the last port of call. Hence Mexico is regarded as the home. On the other hand Ximenes, who lived in Mexico several years, and Hernandez after him, call it the *Chimalacac del Peru*; "acak" I find means a *reed*, and thus refers to the long tall single stem of the cultivated crop. The inference is that the plant as we know it was evolved by ages of selection *in Peru*, by guano fed cultivation, possibly long before Inca rule, the plant having been taken by all migrating tribes from the Mexican district. . . . Regarded as a product of Peruvian agriculture the sunflower is curiously parallel with the *maize*. . . . It was the oil crop of ancient America.

The true *H. annuus* appears to be quite unknown in the wild state, but nevertheless the monocephalic character may have arisen among wild plants. Dr. Church makes the following suggestion:

If the monocephalic form is the giant of cultivation derived from the Prairie form, it should be possible to repeat the history, by growing Prairie forms in quantity, and selecting the suitable mutations when they appear under the stimulus of excess manure (guano for choice). My idea has been that, knowing what to look for, it might be possible to get somewhere near it in say 10 years; though the Indians possibly took 2,000. General structural evidence alone suffices to show that the monocephalic strain is the response to selection for close cultivation (about two plants per square yard). The solitary heads are required for simultaneous harvesting.

2. *H. lenticularis* Douglas. The prairie sunflower, much branched, and normally with dark disc. It has been regarded as the wild type of *H. annuus*, but Rydberg treats it as a distinct species. In crosses with typical *annuus*, the F_1 is intermediate, often with a tendency to fasciation. If *annuus* and *lenticularis* are considered specifically distinct, we have to face the difficulty that the former is known only in cultivation, and its one "specific" character, the monocephalous habit, is not constant.¹ The color of the disc is not a reliable distinction, since yellow discs occur in wild plants. Possibly the variation shown by *H. annuus* may be explained by contamination with *lenticularis*, since some strains, at least, are constant in their characters. At present, however, it seems probable that no wild species ever existed with typical *H. annuus* characters; the actual facts would probably be best represented by considering *lenticularis* the species, and *annuus* a cultivated variety derived therefrom. Since, however, the latter was first named, the species-aggregate will have to be called *H. annuus*, and the nomenclatural outcome will be as follows:

¹ Shull, *Botanical Gazette*, 45, 105, figures a much branched form which is not the wild *lenticularis*.

Helianthus annuus, L.(a) *lenticularis* (Dougl.)(b) *macrocarpus* (D.C.) = *annuus* L., s. str.

At the same time, for ordinary purposes, it may be permissible to simply write *H. lenticularis* when referring to the wild plant.

3. *H. aridus* Rydberg. Like *H. lenticularis*, but leaves lanceolate or narrowly deltoid, minutely toothed or entire. Montana to New Mexico. Nelson calls this a synonym of *H. petiolaris*, which it certainly is not. It must be called *H. lenticularis aridus* (Rydb.) or *H. annuus lenticularis* var. *aridus*, since it is a variable form of *lenticularis*, which may possibly be due to crossing with *H. petiolaris*, the hybrid having crossed back with *lenticularis*. From the mode of its occurrence it is nearly certain that it is not a simple *lenticularis* \times *petiolaris* hybrid, *petiolaris* being often absent from the immediate vicinity.

To give an idea of the actual condition of affairs where *H. aridus* occurs in Colorado, I present a synopsis of the forms found at Longmont, August 30, 1914:

(A) *H. aridus* type; smaller and more slender, with cuneate bases to leaves.

(a) Variety with yellow disc; two plants found.

Disc 19 mm. diameter, light yellow (corollas entirely dull light yellow); rays ordinary; foliage unusually pale; base of leaves rather broad-cuneate, marginal teeth feeble.

(b) Disc dark (corolla lobes dark reddish). Leaves with cuneate base and subentire margins; typical *aridus*. Involucral bracts very broad and bristly. These rather slender plants have small discs (17–21 mm. diam.) and very ample rays, which are not very numerous (10–13); color of rays rich orange yellow; stems lightly speckled with purplish.

(i) Rays longer, about 38 mm. long and 15 broad.

(ii) Rays shorter, about 28 mm. long and 14 broad.

(This difference in size of rays is probably environmental.)

(B) *H. lenticularis* type; bases of leaves truncate or cordate; plants usually more robust; disc dark.

(a) Aspect of *aridus*, being rather slender, with small (diam. 23.5 mm.) disc and long rays; but leaves broadly truncate at base and rather strongly toothed, quite *lenticularis* style. This is a very pretty form, with long rays (about 40 mm. long and 11 broad), more or less twisted at end, and rather narrow. The rays number about 15.

- (b) Aspect of *lenticularis*; more or less robust, rays rather short and numerous.
- (i) Rays comparatively short and broad (about 22 mm. long and 10 broad on a small head), the middle third beneath with its apical half variably light brownish-red. Leaves thick, with broad petioles.
 - (ii) Rays normal.
 - (a) Upper leaves ovate, scarcely at all dentate, inequilateral. Disc small (22 mm. diam.), rather paler than usual, the corolla lobes showing less red. Rays 14, about 31 mm. long and 11.5 broad.
 - (β) Upper leaves broad at base, but somewhat cuneate, rather feebly dentate. Disc 20–23 mm. diameter. A small head (disc 20 mm.) with many (21) quite short rays, about 17 mm. long and 7 broad.
 - (γ) Typical *lenticularis*, with broad-based strongly dentate leaves. Disc 37 mm. diameter; rays 37 mm. long, numerous (about 33).

It would of course be possible to maintain that *H. aridus* was originally a distinct or isolated species, which has now lost its purity by crossing with *lenticularis*. We can at least say this, that if *annuus*, *lenticularis* and *aridus*, in their pure forms, inhabited three different islands, few would hesitate to regard them as perfectly “good species.” Also, if they grow mixed for any length of time, they are sure to suffer from “vicinism” to such an extent as to lose their supposed original distinctness. At present, however, we have no assurance that *H. aridus* has ever constituted a distinct species, in the sense of occupying any considerable area in its pure form. On the other hand, it is manifestly not a “fluctuating variation,” due to mere environmental conditions.

4. *H. petiolaris* Nuttall. Described by Nuttall in 1821, from “the sandy shores of the Arkansa,” and recommended as “an ornamental annual of easy culture.” It extends from British America to the State of Chihuahua. It differs from *H. lenticularis* by (a) smaller stature, (b) leaves differently shaped, lanceolate or broad-lanceolate, not dentate, more or less shiny above, those of *lenticularis* being quite dull, (c) bracts of involucre lanceolate, with margin very short-ciliate. Stem rough, with a little purplish color; basal third of rays deeper orange than the rest.

This is a good species in the ordinary sense; in Colorado it is often found abundantly in the cañons of the foothills, growing without admixture of other species. Lower down, it frequently occurs with *lenticularis*.

The variety *patens* (Lehm.) Rydb. is said to differ by having the heads larger, long-peduncled, the peduncles fleshy toward the top; leaves large, long-petioled. Nuttall described his original *petiolaris* as having the peduncles "of great length," and the petioles "of an extraordinary length," though the leaves were "rather small." Probably *patens* is not far from the original *petiolaris*. Gray considered *patens* a synonym. According to Rydberg, the leaves of *patens* are broadly ovate or subcordate, much in the style of *lenticularis*, while the bracts are those of *petiolaris*, thus reversing the condition of *aridus*. It is possible that *aridus* and *patens* are both remote results of the *lenticularis* \times *petiolaris* cross, but in the vicinity of Boulder, when *aridus* is common, I have not found *patens*.

5. *H. camus* (Britton) Wooton and Standley. A species of New Mexico, Chihuahua, and adjacent regions, close to *petiolaris*, but with abundant white pubescence on leaves and stems. The involucre bracts are of the *petiolaris* type. This is to *petiolaris* much as *H. argophyllus* is to *lenticularis*, but the pubescence is long and spreading, not subappressed and silky.

6. *H. argophyllus* Torrey and Gray. Discovered by Drummond in dry soil in Texas. This has the form and leaves of *lenticularis*, but is very remarkable for the long subappressed silky white hairs, totally different from those of any other *Helianthus* known to me. Gray remarks that it "degenerates in cultivation apparently into *H. annuus*," which merely means that it suffers from vicinism. Old cultivated stocks, kept pure, are quite constant. A remarkable feature of *H. argophyllus* is the extremely slow growth, at least until near flowering time. This peculiarity is dominant in a cross with *H. annuus* \times *lenticularis*.

7. *H. debilis* Nuttall. Florida to Texas.

8. *H. præcox* Engelm. and Gray. Florida to Texas, near coast. Differs from *debilis* by being strongly hirsute.

9. *H. cucumerifolius* Torrey and Gray. Texas. Differs from *debilis* and *præcox* by having the branches mottled with purple.

The last three were eventually reduced by Gray to a single species, but Small keeps them separate. My wife and I have grown *H. cucumerifolius* for several years, and have crossed it with *annuus* \times *lenticularis*. The first cross is quite fertile, but it is impossible to get any quantity of F_2 seed. Mr. Leonard Sutton in England has had the same experience; he writes (April 3, 1915)

We are arranging for a large breadth of the *cucumerifolius* crosses this season, but we have found as you mention that very little seed is produced, and we are hoping that the plant will improve in this respect if grown for a few years, and the best seeding plants are selected for stock.

These hybrids are of considerable horticultural value, especially those derived from crosses with the red sunflower, so it is desirable to secure fertile strains if possible. Something may be attained by crossing back with the parent species.

The *H. cucumerifolius* type is dwarf, freely branching, with broad bright green leaves, shiny on both sides. The involucral bracts are long and narrow. The bulb or swelling of the disc corollas is minutely puberulent, whereas that of the *lenticularis* forms is long hairy. In the F_1 hybrid the bulb is long-hairy as in *lenticularis*, the character being dominant. Although *H. cucumerifolius* is very unlike the other species (except *debilis* and *præcox*) in appearance, its constant structural differences are very few. The base of the leaves, as in the *annuus* forms, may be auriculate or truncate. The disc bracts may be long-ciliate, or with the margins merely appearing scurfy. It is proper to state that my material belonged to cultivated strains; possibly the wild plant is less variable.

Thus we have at the most nine species, which can probably be reduced to five. They belong to the region which used to be marked in old geography books as the "Great American Desert," though members of the *debilis* group extend along the Gulf States to Florida. The dominant, widely distributed form is *lenticularis*, a plant of sandy river-bottoms and similar places, which has spread as a weed in cultivated areas. Prior to the era of cultivation it is probable that *H. petiolaris* occupied a greater area, at least in acreage. At the present time *H. lenticularis* is common in California, but I suspect that it has been introduced into the Pacific coast region by man.

In order to give an idea of the cultivated forms of our group, I have made a table from Sutton's Catalogue for 1915.

Silver-leaved (<i>argophyllus</i> -type); rays yellow;	
disc black; 5 ft.	<i>Silver-leaved.</i>
Not silver-leaved	1.
1. <i>Cucumerifolius</i> -type, none over 4 ft. high.....	2.
<i>Annuus</i> -type, mostly tall	6.
2. Only 12 inches high, compact	<i>Dwarf Miniature.</i>
Four feet high	3.
3. Rays rolled, like the cactus dahlia	<i>Orion.</i>
Rays not rolled	4.
4. Rays pale primrose, disc dark	<i>Primrose Stella.</i>
Rays bright yellow	5.
5. Heads small, with dark disc	<i>Miniature.</i>
Heads larger, rays long	<i>Stella.</i>
6. Rays wholly or partly chestnut red	<i>Red.</i>
Rays wholly or partly vinous	<i>Langley Gem</i>
Rays primrose	7.
Rays bright yellow or orange	9.
7. Double (i. e., disc florets ligulate)	<i>Double Primrose.</i>
Single; disc black	8.
8. Tall, 6 ft. high	<i>Primrose Perfection.</i>
Dwarf, 2.5-3 ft.	<i>Single Dwarf Primrose.</i>
9. Double (i. e., disc florets ligulate).....	10.
Single (i. e., normal heads).....	11.
10. Flowers orange; 6 ft.	<i>Double (also a double 5 ft. high).</i>
Compact habit; 3 ft.	<i>Dwarf Double.</i>
11. Heads extremely large; height 8-10 ft.	<i>Giant.</i>
Heads ordinary or smallish; disc dark; height 6 ft.	12.
12. Heads medium size	<i>Æsthetic Gem (J. Veitch & Sons).</i>
Early flowering	<i>Earliest of All.</i>

Of the above *Red* is *coronatus*, and *Langley Gem* is *vinosus*, both derived from our Boulder cultures. The seed offered as *Langley Gem* was grown in Boulder. The *Primrose* variety I have called *primulinus*.

An old cultivated variety is *H. annuus* var. *indicus* (*Helianthus indicus* Linn., Mant. I, 117), peculiar for the foliar expansion of the involueral bracts. It did not come from India, but from Egypt. *Tithonia speciosa*, once regarded by Hooker as a *Helianthus*, has the bracts normally foliaceous. In 1913 I witnessed the appearance of foliaceous bracts in the F_2 generation from *primulinus* \times *coronatus*. The plant in question was a very abnormal dwarf, wholly unlike the rest of its generation, or any known parents. It was described as follows:

Dwarf, about 28 mm. high; slender, fasciated at top of stem; rays vinous, but on nearly all the heads a very dilute and dingy color; disc dark, stigmatic branches dark red; apical part of disc corollas dark greenish, tipped with red, and very hairy; anthers not projecting, but not shrivelled, almost wholly without pollen, and what there is probably no good; achenes hairy, usually with supernumerary pappus scales; pappus scales stained with pink; involueral bracts long and tapering, strongly hirsute, curled over, one or two outer ones long and foliaceous; stem hirsute; leaves long and narrow, narrowly cuneate at base; margins irregularly, sharply dentate, entire on small very narrow leaves; sometimes one of the large lateral veins of the leaves, and its supporting tissue, absent.

Such a plant may result from some unwonted combination of genes, whereby the normal constitution is broken down and in the resulting disruption characters usually suppressed appear. Such monstrosities quickly perish, but during their transient existence may reveal, like a drunken man, matters which in the well behaved would never reach the surface.

One of the most remarkable of cultivated varieties is the *Chrysanthemum-flowered*, of which we obtained a

perfectly constant and uniform strain from Dreer. It may be named var. *chrysanthemoides*; plants of the same general type have passed in horticulture as var. *californicus* (not *H. californicus* D.C.)

Helianthus annuus var. *chrysanthemoides*

Manner of growth.—(Tested in two seasons). Grows much more slowly than the other forms (except *argophyllus*), but is very robust. Nine plants studied were 15–17 inches high July 14, about 36 inches July 30, and coming into flower at about 5 ft., 6 inches, August 15.

Foliage.—At first (June 8) leaves are narrow and long; very uniform. Later, the upper (small) leaves are conspicuously pallid. At time of flowering the leaves are broad, cordate, with auriculate base; surface very strongly crinkled; margin moderately dentate.

Pubescence.—Leaves soft with very scanty pubescence; petioles somewhat scabrous; stems, especially toward the top and under the heads, with abundant and conspicuous soft white pubescence.

Heads.—Stalks greatly broadened under heads, diameter about 27 mm. just under bracts; involucre bracts hairy, the marginal hairs not longer than those covering the backs of the bracts, five strong veins, and others weak; basal half of bracts about 15 mm. broad, gradually, not abruptly, tapering to acuminate ends; bracts extending about 18 mm. beyond outer florets, which are like the inner ones; heads entirely double (*i. e.*, corollas ligulate), rays very bright orange or saffron, discs light green before they come into flower; immature achenes with much silvery hair.

This plant is so distinct, structurally and physiologically, that if it were not known to have originated in cultivation, it might well pass as a distinct species. Although I have no information concerning its history, I can only suppose that it is part *argophyllus*. Mr. Leonard Sutton writes me that the similar *Double* catalogued by him, which is of continental origin, does not grow more slowly



FIG. 1, above, Double Red Sunflower. FIG. 2, below, *Helianthus von tortuosus*.

than other sunflowers in its early stages. The var. *chrysanthemoides* was found by us to cross freely with the *annuus* \times *lenticularis* varieties, producing a series of semi-doubles. The double and semi-double forms extracted from this cross and from crosses with Sutton's various double forms need not be described here, but in order to illustrate the double type, I give a figure of a full double with chestnut color, the red being derived from the variety *coronatus* (Fig. 1).

MODIFICATIONS OF THE RAYS

Number.—Halsted (Rept. Bot. Dept. N. J. Agric. Exp. Sta. for 1911, pp. 335–337) has given elaborate data from the branched form of the cultivated *H. annuus*, showing that the terminal heads have most rays, and when there are many lateral branches, the rays on these are comparatively few. Nevertheless, there are inherited differences in the number of rays, not depending on conditions of nutrition. I observed a striking case by the roadside in Boulder, where three wild *lenticularis* plants, growing close together, differed thus:

- (a) Rays normal, at right angles to axis; number of rays in well-formed heads, 21, 21, 21, 21, 20, 21, 21.
- (b) Rays normal, elevated, their plane oblique in relation to the axis of head; rays in well-formed heads, 14, 13, 14, 14, 14, 11, 15.
- (c) Rays set obliquely, but less so than in *b*; rays in well-formed heads, 18, 18, 18, 19. In this plant many of the rays were modified by quilling and splitting, some being completely quilled, *i. e.*, hollow and tubular. The normal rays were very obtuse, and distinctly emarginate at end. Some showed a little red color on apical part of middle third beneath.

Length.—The length also differs, the differences due sometimes to race, sometimes to illumination or nutrition. In our cultures mutational forms have arisen with unusually short rays, thus:

- (a) Var. *vinosus* with disc 55 mm. broad, rays only 35 mm. long; disc unusually convex.

- (b) Var. *bicolor* with disc 64 mm. diameter, rays only 29 mm. (Next to it, in the same lot, grew a plant with disc diameter 38, rays 47 mm.)

These measurements represent average heads from the respective plants. A quite analogous variation was seen in two plants of *Ratibida columnifera*, growing at Boulder along with the typical form (var. nov. *breviradiata*, rays yellow, only about 10 mm. long, about half the normal size).

Torsion.—A peculiar form which appeared in our cultures is the variety *tortuosus*, in which the ends of the rays are twisted, as though in curl papers. This is wholly unattractive, but other variations have the long rays moderately curled or twisted, promising the development of a series of forms analogous to the cactus dahlias. As with the cactus dahlias, the rays may be rolled instead of twisted; a wild form of this type may be described thus:

Helianthus lenticularis var. n. *angustus*. Rays about 20, narrow, rolled, so that they are separated by wide intervals. The rays were 36 mm. long and 5 wide (a normal *lenticularis* ray 30 mm. long is 9 wide). Disc 26 mm. diameter. Goodview, Colorado, July 28, 1913.

Tubular Rays.—Under the heading "Number" above, a case of completely quilled rays in a wild sunflower is recorded. This peculiar modification indicates some deep-seated tendency in the Compositæ, since it appears in several genera, *e. g.*:

- (a) *Ratibida columnifera* var. n. *tubularis*. Rays of the usual orange color, about 25 mm. long and 3.5 broad, completely quilled, being hollow cylinders. Flagstaff Hill, Boulder, Colorado, July 19, 1914.
- (b) *Rudbeckia hirta* var. *tubuliforme* S. H. Burnham Amer. Botanist, Feb., 1914.
- (c) *Gaillardia pulchella* var. *fistulosa* (*G. fistulosa* Hort.).

Emarginate and Cleft Rays.—This is another common modification, also observed in other genera, as *Ratibida* (*R. columnifera* var. n. *incisa*; rays with one or two deep

incisions, and also some narrow supplementary rays; Boulder, Colorado, August 8, W. P. Cockerell).

Double Rows.—The disc remaining normal, the rays may be in two rows, indicating an approach to a type resembling the star dahlias.

Color.—The yellow may be of various shades from deep orange to very pale, approaching white. This has already been discussed in *Science*, August 21, 1914, pp. 283–285. It may be possible eventually to get a pure white. Dr. Church (in litt.) refers to a white form as having been mentioned long ago by Hernandez. There is also the development of the soluble (anthocyanin) red pigment, giving us the chestnut red and wine red varieties.

CONCLUSIONS

It is impossible at the present time to give all the evidence on which opinions have been formed, but such facts as are reported above, and others, seem to suggest the following generalizations:

1. The number of genes or determiners in *Helianthus* is not infinitely great; it is probably very much less than exists in most animals, and the study of the processes of heredity is relatively simple.

2. In the history of the sunflowers of the *H. annuus* group, there have been few really new developments. Species which seem very distinct prove on examination to have few special characters of their own.

3. It is quite common for variations to arise, in wild and cultivated plants, which appear to break the type, and initiate something altogether new. When, however, we begin to gather data on the variation of the Compositæ, we find that practically all these “new” variations repeat themselves in various species, and at various times, indicating that they represent deep-seated common tendencies. Their occurrence among wild plants shows that they are not necessarily connected in any way with cultivation, and it is equally evident that they need not indi-

cate any sort of hybridization. For example, *Ratibida columnifera* presents many variations parallel with those of *Helianthus*, in localities where it is the only species of its genus.

4. We are led, then, to think of the annual sunflowers as plants representing a certain complex of potentialities or genes (of which we may hope at length to make a reasonably complete catalogue), offering these in different combinations at different times, usually failing to register any permanent advance, but once in a long while reaching a new position of stability, suited to a particular environment. These positions of stability represent what we call the species. As with the dahlia, the horticulturist may expect to be able to produce many interesting varieties by selecting and saving the various possible combinations, but analysis shows that the genes going into these are the old ones, the effects of which may be seen from time to time even in wild plants.

The perennial sunflowers appear to offer a more complex problem. Mr. S. Alexander has found hundreds of what are considered "elementary species" in Michigan. He has been good enough to send me a large number of these, and I can testify that they are appreciably different; yet they seem to represent recombinations of old characters, already known to exist in the species of the manuals. Some would dismiss them, along with the multitudes of *Cratægus*, as hybrids; but it does not seem justifiable to assume hybridization without better evidence. We have sufficient proof, I think, that all sorts of new combinations of characters may arise within a type, without hybridization.

Undoubtedly new determiners are formed (how, we need not here speculate) from time to time, but the occurrence must be so rare and so difficult to demonstrate that we can hardly hope to obtain satisfactory evidence concerning it.